

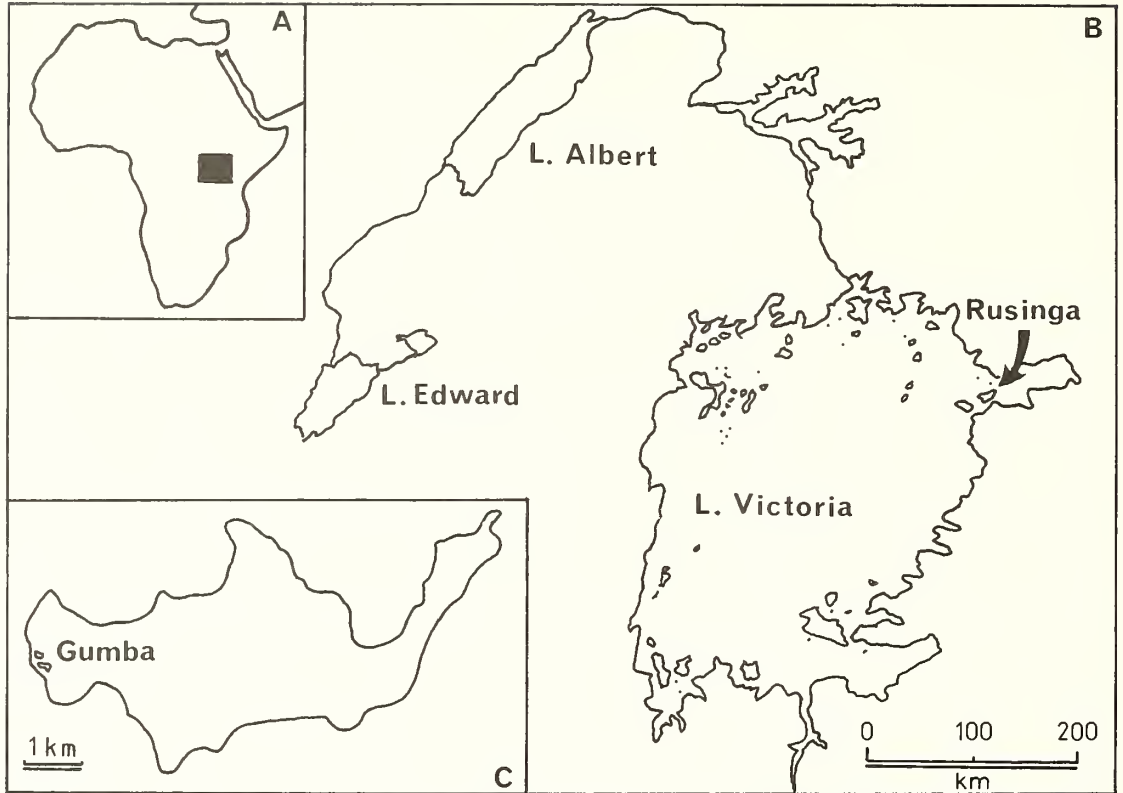
BIOGEOGRAPHY AND EVOLUTION OF AFRICAN FRESHWATER MOLLUSCS: IMPLICATIONS OF A MIOCENE ASSEMBLAGE FROM RUSINGA ISLAND, KENYA

by P. W. KAT

ABSTRACT. A freshwater mollusc fauna from the Early Miocene Gumba beds of Rusinga Island, Kenya, is re-examined. The fauna consists largely of mutelid bivalves, and two new species of the genus *Pleiodon*, *P. lanceolatum* and *P. rusingae*, are described. The Gumba fauna is compared with those of the contemporary Mohari Formation of the Edward-Albert Rift and the early Miocene Turkana Grits in northwestern Kenya. None of the early Miocene freshwater faunas thus far described contains representatives of the presently widespread and diverse bivalve family Unionidae and gastropod family Viviparidae. Ancestors of the recent African viviparids and some of the unionids are proposed to have been introduced when Africa and Eurasia were joined by closure of the Tethys Sea. The Miocene faunas are also uninformative as to the origins of the distinctive endemic mollusc fauna of Lake Tanganyika. Collectively, however, these faunas provide valuable insight into African freshwater molluscan species diversity during the Miocene, and relationships between Miocene and extant taxa.

THE pre-Pleistocene fossil record of African freshwater mollusc faunas remains little investigated despite their potential to provide information on molluscan biogeography, evolution, and origins of endemic assemblages of the older great lakes such as Tanganyika and Malawi (Fuchs 1936; Darteville and Schwetz 1948; Gautier 1965, 1970; Lepersonne 1970). Faunas of the Miocene are perhaps best known, and have been collected from three main areas: the Edward-Albert Rift (the Mohari Formation; early Miocene by mammalian faunal inference; see Gautier and Van Damme 1973), near Lake Turkana (the Turkana Grits, age estimated between 17 and 23 my; see King and Chapman 1972; Van Couvering and Van Couvering 1976), and around the Winam Gulf area of Lake Victoria (especially the Gumba Beds on Rusinga Island, age estimated at 19 my; see below) (Verdcourt 1963; Gautier and Van Damme 1973; Van Damme 1984). These Miocene faunas largely predate the establishment of the major African rift systems, and are thought to be contemporary with taxa ancestral to the distinctive endemic mollusc fauna of Lake Tanganyika (Fuchs 1936; Gautier 1967; Beadle 1974; Andrews and Van Couvering 1975). Also, pre-rift drainage patterns are thought to have linked the Zaire (Congo) River with large areas of eastern Africa (e.g. Cooke 1958; Fryer and Iles 1972; Beadle 1974), and taxa of the Mohari mollusc fauna have been proposed to be conspecific with taxa of the Gumba Beds (Gautier 1967; Gautier and Van Damme 1973).

The Miocene and largely Pleistocene freshwater molluscs of the Edward-Albert Rift have been well described (e.g. Adam 1957, 1959; Gautier 1965, 1966, 1970; Lepersonne 1970; Gautier and Van Damme 1973). In contrast, the Rusinga freshwater fossils were only examined by Verdcourt (1963), and proposed similarities between the two faunas were based largely on incomplete or fragmentary specimens. Since Verdcourt's (1963) initial description of this fauna, several other collections have been made and deposited in the Division of Palaeontology of the National Museums of Kenya. These subsequent collections constitute a marked improvement over the poor material available to Verdcourt, and have both clarified relationships between the two faunas and their levels of diversity.



TEXT-FIG. 1. Location of the Gumba Beds on Rusinga Island, Lake Victoria, Kenya.

ENVIRONMENT AND AGE OF THE GUMBA BEDS

The freshwater molluscs examined here occur in the Gumba Beds on the western part of Rusinga Island (text-fig. 1). The fossils occur in lenticles of coarse sand/gravel consisting of very poorly sorted, angular particles indicative of a relatively high-energy depositional environment such as a stream channel. Most of the shells are fragmentary. *In situ* 'reefs' of the freshwater bivalve *Etheria elliptica* occur in the same and underlying deposits, all of which lie between the Rusinga Agglomerate (19.5 my; Basal Agglomerate of Kent 1944) and the Hiwegi Formation (17 to 18.5 my; Tuffaceous Series of Kent 1944), and are contemporary with the 'Unnamed Formation' (19 my; Argillaceous Series of Kent 1944) (dates in Van Couvering and Miller 1969). In addition to the gravels, the beds also contain a variety of other aquatic deposits such as sandstones and deep water greenish siltstones. Kent (1944), Bishop (1963), and Temple (1969) generally agree on the existence of one or a series of lakes in the region formed by volcanic damming of drainages. These Miocene lakes, however, were not ancestral to Lake Victoria, which was formed much later as a result of the development of the African rift systems, uplifting, and the formation of volcanic fields which reversed some of the westward flowing drainages of the region (Bishop 1965; see Kendall 1969 for a general background description of the formation of Lake Victoria).

SYSTEMATIC PALAEOLOGY

Superfamily UNIONACEA

Family MUTELIDAE

Genus ETHERIA

Etheria elliptica Lamarck, 1807

Text-fig. 2F

Discussion. This is the most common bivalve species present, occurring in *in situ* 'reefs', and as articulated and fragmentary valves within the gravels. The species is presently widely distributed within Africa, occurring in the Nile, Zaire (Congo), and Niger River basins as well as on Madagascar. It is not known from Lakes Tanganyika and Malawi, but occurs in large numbers in Lake Victoria.

Material. Twenty-two single and three articulated valves.

Genus PLEIODON

Pleiodon moharensis (Gautier, 1965)

Text-fig. 2E

1963 *Iridina* sp., Verdcourt, p. 31, fig. 63a, b.1963 *Mutela* sp., Verdcourt, p. 30, fig. 62.1965 *Iridina* (*Pliodon*) *moharensis* Gautier, pp. 144–146, pl. 6, figs. 5–7; pl. 7, figs. 1, 3, 5.1965 *Iridina* (*Pliodon*) *subelongata* Gautier, pp. 146–147, pl. 7, figs. 7 and 8; pl. 8, fig. 3.

Discussion. This is the largest *Pleiodon* species present, with an elongate ovate shell. The valves are compressed to subcompressed, and solid in large specimens. The anterior end is regularly rounded, and the posterior end often squared or bluntly rounded. The ventral margin is straight to slightly concave in large specimens; the dorsal margin is generally straight. A broadly rounded posterior ridge is present. The umbos are low and situated in the anterior third of the shell. Shell sculpture consists of concentric striae. The dentition is taxodont and well developed, consisting of straight teeth set at a slight angle to the hinge anterior to the umbo. Anterior adductor and retractor scars are deep, and dorsal retractor scars are set below the umbo. The posterior adductor scar is distinct, and the posterior retractor scar is well separated from that of the adductor. The pallial line is usually distinct.

Material. Sixteen partial valves, one complete valve.

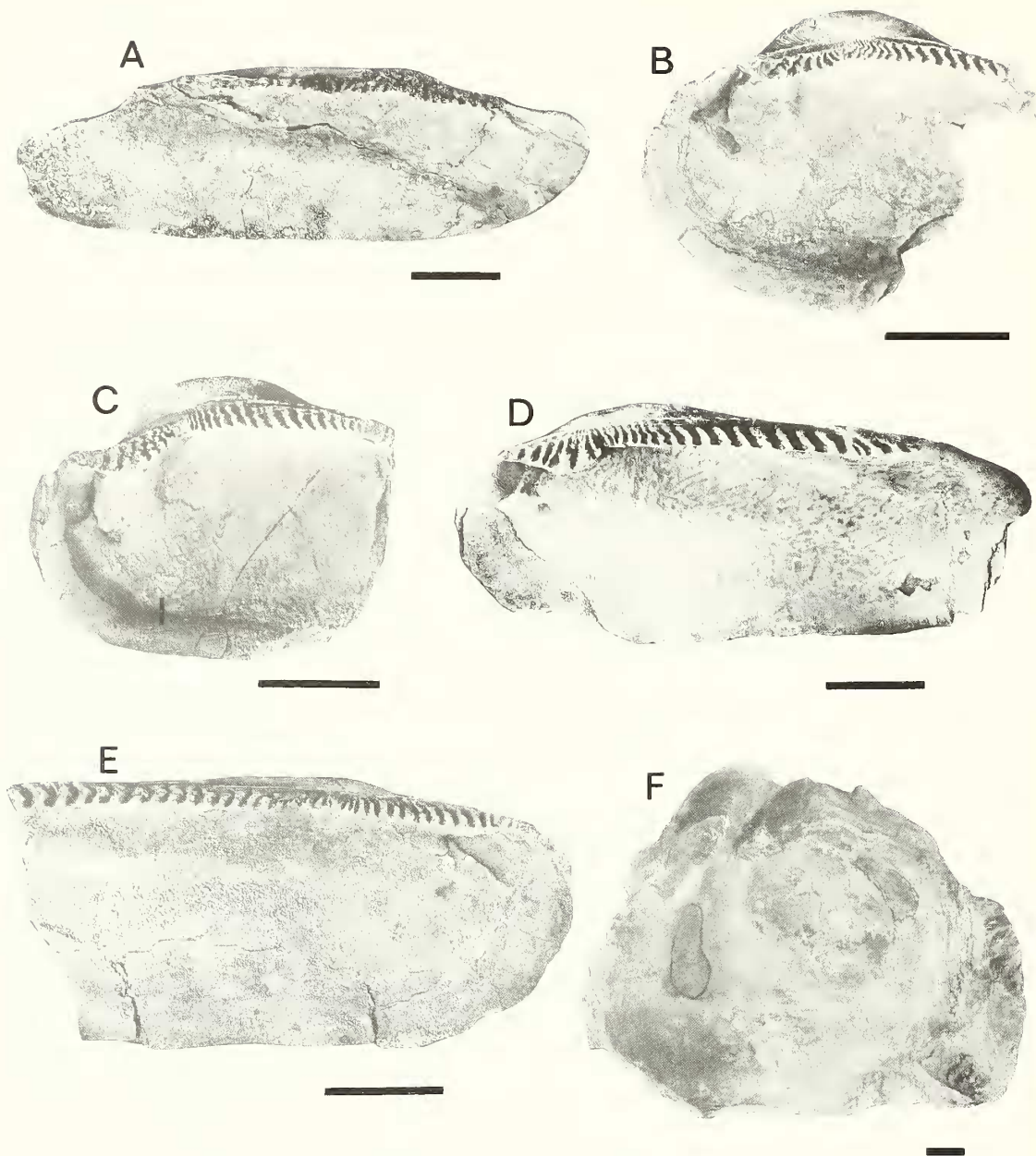
Occurrence. This species is also known from the Mohari Formation in the Edward–Albert Rift (Gautier and Van Damme 1973), and was postulated by Gautier (1966) to be closely related (ancestral?) to recent *P. spekii* from Lake Tanganyika.

Pleiodon tavernieri (Gautier, 1965)

Text-fig. 2B, c

1963 *Caelatura* sp. Verdcourt, p. 30, fig. 61.1965 *Iridina* (*Pliodon*) *tavernieri* Gautier, pp. 138–140, pl. 4, figs. 5 and 7; pl. 5, figs. 1, 2, 4, 5, 7.1970 *Pliodon* (*Pliodon*) *tavernieri* Gautier, p. 123, pl. 5, fig. 7.

Discussion. This is the smallest bivalve species represented, and is variable in shape between subtriangular and ovate. Specimens are generally subinflated, with a straight or slightly curved ventral margin and a rounded anterior margin. A posterior ridge is well defined, especially in the subtriangular specimens, where the posterior end is pointed. The umbos are full, project above the hinge line, and are located in the anterior one-third to one-half of the shell. Shell sculpture consists of fine radial lines. The dentition is taxodont, and the hinge plate is relatively straight posteriorly but curved anteriorly. The teeth are irregular anterior to the umbo, and become chevron-shaped posteriorly. The beak cavities are deep, and dorsal muscle scars are visible under the hinge plate. The



TEXT-FIG. 2. The mutelid bivalve species of the Gumba Beds. A, *Pleiodon lanceolatum* (holotype, KNMI-RU-16814). B, C, *P. tavernieri* (KNMI-RU-14840, 14835). D, *P. rusingae* (holotype, KNMI-RU-16815). E, *P. moharensis* (KNMI-RU-16811). F, *Etheria elliptica* (KNMI-RU-16809A). All scale bars = 1 cm.

anterior adductor and retractor muscle scars are deep and the pallial line distinct. The shell can become thick in large specimens.

Material. Fifteen partial and three articulated valves.

Occurrence. This species also occurs in the Mohari Formation (Gautier and Van Damme 1973), where the specimens are apparently less triangular than those from Rusinga.

Pleiodon lanceolatum sp. nov.

Text-fig. 2A

Description. A medium-sized, very elongate ovate shell more than three times as long as high, moderately inflated. The anterior and posterior ends are pointed, and the dorsal and ventral margins are straight. A well-developed posterior ridge is present. The umbos are low and situated in the anterior third of the shell. The hinge plate is very narrow and set with fine taxodont dentition especially anterior to the umbo. Posterior to the umbo, the teeth consist of delicate, rather rounded chevrons. The beak cavities are shallow, and the dorsal retractor muscle scars are located posterior to the umbo. The anterior retractor and adductor muscle scars are distinct, the pallial line is faint, and the posterior adductor and retractor scars not present in the type specimen. The species differs from other known *Pleiodon* by its elongate shape, pointed anterior end, and delicate dentition.

Material. Holotype KNMI-RU-16814 consisting of a single, partial left valve.

<i>Dimensions</i> (in mm).	Length	Width
KNMI-RU-16814	58	18

Pleiodon rusingae sp. nov.

Text-fig. 2D

Description. A medium-sized, subcompressed, elongate ovate shell more than twice as long as high. The anterior end is regularly rounded, and the posterior end bluntly pointed. The ventral margin is straight or very slightly curved. The dorsal margin is straight and the posterior ridge well defined. The umbos are low, situated in the anterior quarter of the shell. Dentition is taxodont, and the hinge plate short and curved anterior to the umbo. Posterior to the umbo, the hinge plate is straight and set with regular, strong teeth lying at an angle to the hinge line. The beak cavities are shallow, and the dorsal retractor muscle scars are set posterior to the umbo. The anterior adductor and retractor muscle scars are deep and the pallial line is well defined. The posterior adductor scar is well defined, and separated from the posterior retractor scar. The species differs from other *Pleiodon* described mainly by its distinctive short and curved anterior hinge plate.

Material. Holotype KNMI-RU-16815; Paratypes KNMI-RU-16817, 16818, 14818, 14834.

<i>Dimensions</i> (in mm).	Length	Width
KNMI-RU-16815	70	25

Order MESOGASTROPODA

Family AMPULLARIIDAE

Genus PILA

Pila ovata Olivier, 1804

Discussion. The single gastropod species from the Gumba Beds is only known from opercula. Verdcourt (1963), however, mentions that shells of this species and those of the related ampullariid *Lanistes carinatus* were collected from other localities on Rusinga Island. Both species are also known from the Mohari Formation (Gautier and Van Damme 1973). The present geographic range of *Pila ovata* extends from Egypt to northern Mozambique and westwards to Nigeria (Brown 1980).

Material. Eight opercula.

TABLE 1. Freshwater Molluscan faunas of the Miocene East African sites mentioned in the text

Rusinga Island (c. 18-23 my)	Turkana Grits (c. 17-23 my)	Edward-Albert Rift (early Miocene)
BIVALVES		
<i>Etheria elliptica</i>		<i>Etheria elliptica</i>
<i>Pleiodon moharensis</i>		<i>Pleiodon moharensis</i>
<i>P. tavernieri</i>		<i>P. tavernieri</i>
<i>P. rusingae</i>		
<i>P. lanceolatum</i>		
	<i>Pleiodon</i> sp.	
	<i>Mutela</i> sp.	
		<i>Aspatharia triangulata</i>
		<i>Corbicula consobrina</i>
GASTROPODS		
<i>Pila ovata</i>	<i>Pila ovata</i>	<i>Pila ovata</i>
<i>Lanistes carinatus</i>	<i>Lanistes carinatus</i>	<i>Lanistes carinatus</i>
<i>Melanooides tuberculata</i>	<i>Melanooides tuberculata</i>	<i>Melanooides tuberculata</i>
	<i>Saulea</i> sp.	

Sources: Verdcourt (1963); Gautier and Van Damme (1973); Van Damme (1984).

DISCUSSION

East African Miocene freshwater faunas appear to consist mainly of mutelid bivalve taxa such as *Aspatharia*, *Pleiodon*, and *Etheria*, and prosobranch gastropod taxa such as *Lanistes*, *Pila*, *Gabbiella*, *Cleopatra*, and *Melanooides* (Table 1). All these taxa with the exception of *Pleiodon* remain widely distributed in Africa. Among the bivalves, *Etheria* is an apparently monotypic genus with a wide distribution, although soft part anatomy and molecular genetics of widely separated populations have not been compared. *Aspatharia* has diversified into an as yet unknown number of species (48 according to Pilsbry and Bequaert 1927; 9 according to Haas 1969), some of which are ostensibly widely distributed, while others are endemic to single lakes such as Victoria and Malawi. Among the gastropods, *Pila*, *Lanistes*, and *Melanooides* are also encountered outside Africa (e.g. Brandt 1974; Smith and Kersaw 1979; Brown 1980). *Lanistes* (19 African species) and *Melanooides* (27 African species) are especially diverse (Brown 1980). The 20 species of *Cleopatra* and 22 species of *Gabbiella* listed by Brown (1980) are essentially African; a few species in each genus are widely distributed, but many are confined to particular localities or lakes.

Pleiodon is poorly represented in extant African freshwater faunas. The fossil record of the genus dates back to the Upper Cretaceous, where two taxa are encountered in the Nubian Sandstone near Aswan in Egypt (Cox 1955). With the addition of two new species from the Gumba Beds, the number of *Pleiodon* taxa described from the Miocene has increased to four (an undescribed species from the Turkana Grits could increase this total; see Van Damme 1984). *P. moharensis* and *P. tavernieri* apparently were widely distributed in pre-rift drainages. The more restricted occurrence of *P. lanceolatum* and *P. rusingae* could either be indicative of habitat differences between the sites or the occurrence of endemic taxa in the Miocene Winam Gulf area lakes. *Pleiodon* had further diversified by the Pleistocene: early Pleistocene Edward-Albert rift deposits contain six species, including *P. tavernieri* and *P. moharensis* (Gautier 1970). Elsewhere, *Pleiodon* sp. occurs in the Plio-Pleistocene Koobi Fora formation near Lake Turkana (Williamson 1981). This diverse assemblage declined

during the later Pleistocene, and *Pleiodon* is now represented by two species with relictual distributions: *P. spekii* in Lake Tanganyika (previous distribution: Edward-Albert rift (Gautier 1970) and Lake Kivu (Darteville 1948)) and *Pila ovata* in West Africa (previous distribution: Edward-Albert rift (Gautier 1970)). Pain and Woodward (1964) describe an additional West African species, *P. waterstoni*, but I agree with Gautier (1966) that this is probably an ecotypic variant of *P. ovata*.

The Rusinga deposits lack representatives of *Aspatharia*, *Gabbiella*, *Cleopatra*, and *Melanooides*, taxa reasonably common in the Edward-Albert rift (Gautier and Van Damme 1973). These differences could be due to dissimilarities in the habitats represented: the Mohari Formation has been hypothesized to represent a marshy environment close to a river (Gautier and Van Damme 1973), and the fauna is dominated numerically by taxa such as *Lanistes* and *Cleopatra*, which presently occur in swamps and slowly flowing rivers (Brown 1980). In contrast, the coarse, poorly sorted sediments and the predominance of *E. elliptica* (which is very rare in the Mohari) indicates a fluvial and higher energy environment for the Gumba Beds. *Melanooides* occurs in contemporary sediments at Nyakach, about 50 km east of Rusinga (pers. obs.).

Entirely absent from all early Miocene deposits examined to date are representatives of the presently widespread and diverse bivalve family Unionidae and gastropod family Viviparidae. It is possible that ancestors of some of the present African unionids (especially the genus *Caelatura*) and all viviparids were introduced after these deposits were formed, when Africa and Eurasia were joined by the closure of the Tethys Sea (e.g. Dewey and Bird 1970; Andrews and Van Couvering 1975). This event is also thought to have mediated the introduction of several mammal taxa (Cooke 1968), all African cyprinid fishes (Bowmaker *et al.* 1978), a large number of the present Pan-Ethiopian freshwater invertebrates other than molluscs (Harrison 1978), and many flowering plant taxa (Smith 1973).

Newton (1920) and Prashad (1928), however, consider the Viviparidae to have been present on ancient Gondwanaland, based on the occurrence of an upper Cretaceous (Tertiary according to Darteville 1948) 'viviparid' in southern Africa, and a high degree of similarity between African and Indian viviparid species. Later, Rennie (1943) described 'viviparid' taxa from the Early Jurassic of Mozambique. All these fossils, however, are poorly preserved, and seem more likely to be representatives of *Cleopatra* (Thiariidae) which Prashad (1928) included in the Viviparidae. *Cleopatra* was widespread in the Miocene, and now occurs throughout Africa and Madagascar. The earliest unambiguous viviparid taxa (*Bellamyia* and *Neothauma*) occur in Pliocene deposits (e.g. Gautier 1970; Williamson 1981; Van Damme 1984).

The present distribution (text-fig. 3) and fossil occurrences of the Viviparidae outside Africa also argue against their presence on Gondwanaland. In South America, viviparids are only known from the Palaeocene, and these representatives became extinct a short time later. Parodiz (1969) believes these viviparids, as well as other elements of the South American Palaeocene molluscan fauna, to have been derived from North American ancestors at the end of the Cretaceous. Similarly, viviparids are unknown from Madagascar, and apparently have no fossil record in Australia (Prashad, 1928). Smith and Kersaw (1979) believe the present viviparid fauna, as well as several other Australian freshwater molluscs, to have been derived from Asian ancestors in relatively recent times. The similarity between Recent Indian and African viviparids is more likely to have resulted from shared ancestry with a taxon that invaded Africa relatively recently than shared ancestry with a Gondwanaland taxon. Molecular genetic and karyologic data support a relatively recent divergence among African viviparid taxa.

The taxonomy of the numerous recent *Caelatura* species and their relationships to unionid taxa outside Africa is poorly understood. Unambiguous fossil *Caelatura* are, like viviparids, first encountered in Pliocene and Pleistocene deposits. Recently, Heard and Vail (1976) placed southern African *Cafferria caffra* in the genus *Unio* (Unionidae) based on shell sculpture, some soft-part anatomy, and larval and reproductive characteristics. *Unio* s.s. is otherwise only known from the Palearctic and Heard and Vail suggest the south African taxon to be a 'biogeographic relict'. Regardless of its generic placement (see Mandahl-Barth 1982), *Cafferria* appears to have a fossil record dating to the Upper Cretaceous in the Transvaal (Modell 1964), which would imply a long-standing

presence of some unionid taxa in Africa. Similarly, three endemic and monotypic unionid genera (*Brazzaea*, *Pseudospatha*, and *Moncetia*) occur in Lake Tanganyika, and one monotypic genus (*Prisodontopsis*) is endemic to Lake Mweru (Pain and Woodward 1968; pers. obs.). The Tanganyika unionids exhibit anatomical evidence of shared ancestry (pers. obs.), but their relationship to *Prisodontopsis* and *Cafferia* is unknown. All five taxa, however, clearly represent a distinct and separate group of unionids from *Caelatura*, but much more fossil evidence is necessary to elucidate their origin and past distributions.



TEXT-FIG. 3. Distribution of extant members of the gastropod family Viviparidae (based on Starobogatov 1970).

Also missing from the East African Miocene faunas are gastropods that could elucidate the origin of the thalassoid gastropod assemblage of Lake Tanganyika. This highly distinctive group consists of about twenty-five conchologically diverse species distributed among sixteen largely monotypic endemic genera (no other African lake appears to contain even a single endemic snail genus), and is thought by Brown (1980) to have originated from Miocene thiariid taxa living in central Africa before formation of the lake. Brooks (1950) and subsequent authors such as Boss (1978) believe the thalassoid snails to have evolved entirely within Lake Tanganyika, and thus to represent an ancient endemic radiation in which morphologic differentiation has transcended the species level. While the fossil record indicates that several mollusc taxa now endemic to the lake previously had more extensive geographic ranges (e.g. the viviparid *Neothauma tanganyicense* which is found in Pleistocene deposits of the Edward-Albert rift and Lake Rukwa (Cox 1939; Gautier 1970); species of the thiariid genus *Lavigeria* which are also found near Lake Rukwa (Cox 1939); and *Pleiodon spekii* mentioned above), there is to date no fossil evidence of thalassoid species having occurred outside the Tanganyika basin. The soft-part anatomy of these snails is presently too imperfectly known to determine if there exist shared anatomical characters (e.g. see Davis' (1979) analysis of the conchologically variable Mekong River triculine gastropods) indicative of a truly endemic radiation, and biochemical data which could indicate a possible shared genetic identity are in the early stages of being gathered. The origin and evolution of the thalassoid snails must therefore remain speculative at this point.

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